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The Phenology of Macrofungi in Relation to Autumn Rainfall in the Adelaide Hills

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Abstract

Macrofungal species richness and frequency of fruiting was investigated in relation to environmental conditions, early in the rainy season in Cleland Conservation Park in the Adelaide Hills. At two sites: a fern gully and an open woodland, eight permanent 25m^2 quadrats were sampled fifteen times between May and July, 1992. The influence of local temperature, rainfall patterns and soil moisture were assessed. Seventy-three basidiomycete and six ascomycete taxa were collected; the basidiomycete taxa representing five families, dominated by the gilled fungi. There was a strong temporal effect on fruiting pattern which was also correlated with rainfall and temperature during the sampling period. Early in the season there were clear differences between the fungal communities at the two sites, but as the season progressed, they converged towards more similar species compositions.

Introduction

In the dry climate of South Australia, macrofungal fruiting bodies are conspicuous during the cool wet months. Fungi are the major agents of decay, and exist in areas where decomposable material is present. Due to the close association fungi have with their external environment, fungi have been used as generalist organisms in the investigation of ecological processes (Ingold 1984). However, most ecological work on fungi focuses on their hyphal distribution and growth patterns (Park 1968). Fungi are notable for their prolific reproduction and rapid dispersal of large numbers of spores (Ingold 1984). Spore production is important for fungi because of the discontinuous distribution of most fungal substrates (Park 1968). Therefore, to elucidate the survival processes of many fungal species, a knowledge of their fruiting behaviour is required.

Many studies have considered the production of spore producing structures of fungi in Europe (summarised in Wicklow and Carroll 1981; Winterhoff 1992), however, little has been published on the influence of environmental factors on the fruiting of macrofungi in Australia. Chief factors influencing spore production in fungi are temperature and water availability. Temperature effects metabolism and the assimilation of nutrients. Moisture content indirectly controls nutrient availability and subsequently the intensity of spore production (Austwick 1968).

Local environmental gradients in substrate availability and canopy cover influence moisture availability and nutrient supply and therefore species composition. Many ectomycorrhizal basidiomycetes exhibit differences in composition related to forest type (e.g. Bills *et al.* 1985). In Norway, studies have demonstrated that rich fructification is ultimately dependent on the supply of decomposable organic matter after initiation by

heavy rain. High yields require high concentrations of soluble nitrogen and phosphorus. Once nutrients have been depleted in one area, production is low in subsequent seasons regardless of rainfall (Mehus 1986).

To investigate the macrofungal species richness and frequency of fruiting in large scale environmental conditions, a study was carried out in the Adelaide Hills. This study investigates the macrofungal species richness and frequency of fruit body production following heavy autumn rainfall in the Adelaide Hills, South Australia. A comparison was made between areas of different canopy cover to investigate whether general environmental factor such as temperature and rainfall had a greater influence on fungal fruit body production than local conditions such as soil moisture and site exposure. Due to the winter wet period in the Adelaide region, the study was initiated prior to the rain season, during late Autumn.

Materials and Methods

Study sites were at Waterfall Gully, in Cleland Conservation Park in the Adelaide region, South Australia (Fig. 1a). A number of creeks flow through this area during winter, and it is well vegetated producing moist sheltered conditions. Following heavy rainfall during May, 1992, regular visits were made to Waterfall Gully to determine the beginning of the fungal fruit body season and the areas where fungi were growing. From late May, formal records of the number and species of fruiting bodies were made.

To demonstrate differences in fruiting between areas with different canopy cover, a fern gully with dense canopy cover, and a more open shrubland area were sampled. Both sites were in close proximity to the creek bed (Fig. 1b). At each site, eight permanent quadrats of 25 m^2 were pegged out around the creek bed, the quadrats at each site covering a range of heavy clay and sandy soils and containing a variety of fungal substrates such as soil, leaf litter and fallen trees. As far as possible, the quadrats were square (5 x 5 m), but in several cases, the quadrat shape had to be altered to allow for local topographic variation.

The total number of the fruit bodies of each macrofungal taxon within each quadrat were recorded every 3–4 days for an eight week period (15 visits). To minimise recounting of thalli on successive visits, only fruit bodies with no signs of decomposition, liquefication or insect damage were recorded, with the total thallus number per quadrat recorded for each species. To gain a measure of relative soil moisture, soil was collected from each quadrat in an airtight container. A pre-weighed No. 48 filter paper was placed in the container and left to equilibrate for 48 hours. The filter paper was brushed of excess soil, weighed, dried to constant weight and reweighed (Greacen 1989). Daily rainfall and temperature measurements were taken from records provided by the Department of Environment and Natural Resources rangers at the Cleland Wildlife Park, 500 m from the sampling sites.

Each time a new taxon was encountered, characteristic morphological features were recorded in the field following the methods of Cole *et al.* (1985), and specimens were later dried at 70°C. For gilled fungi, a spore print was obtained by placing the cap of each specimen on a piece of coloured paper for 6 hours. These prints were then used to assist identification (Cleland 1934–35; Cole, *et al.* 1985). The spores of some specimens were further analysed for size and shape to clarify identification (Young 1986). Following identification, specimens were also compared for verification with the collections in the State Herbarium of South Australia (AD), and the specimens collected in the present study were deposited there.

These data resulted in a matrix of total fruit body frequencies for each fungal species within each quadrat for each sample time (203 samples and 79 species). A multidimensional scaling analysis was performed to summarise changes in the species and

frequency of fruiting bodies within each quadrat over time using the SSH module of PATN (Belbin 1992). An association matrix using the Bray-Curtis Association measure, together with a dendrogram created using an unweighted pair group mean association (UPGMA), was used to cluster quadrats of similar fungal composition. Nine environmental parameters and population characteristics were used to assist in the interpretation of associations presented in the ordination: (1) rain24: total rainfall within the previous 24 hours prior to sampling, (2) rain: total rainfall between samples, (3) days since rain: number of days since it had last rained at the time of the sampling visit, (4) temperature: the previous day's maximum temperature, (5) moisture: the relative soil moisture within each quadrat, (6) suction: the relative soil moisture retention capacity (7) richness: species richness, (8) abundance: species abundance of fruit bodies within each quadrat over time, (9) time: sampling time.

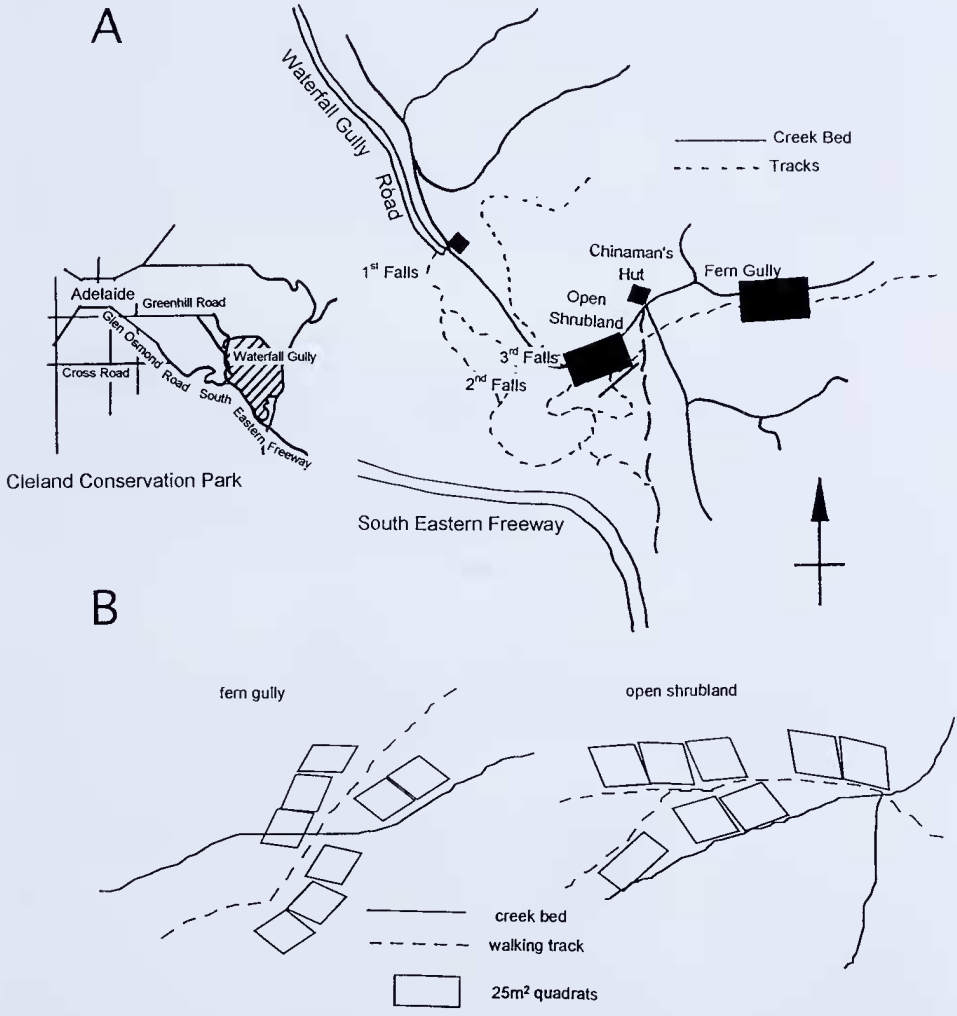

Fig. 1. **a** Map showing the position of Waterfall Gully in the Cleland Conservation Park, Adelaide, South Australia; **b** the position of permanent quadrats in fern gully and a more open shrubland areas. At each site, eight permanent quadrats of 25 m^2 were pegged out around the creek bed.

By multiple linear regression, each of these nine variables is presented as a vector illustrating the direction of increasing effect within the ordination space (Belbin 1991). This was carried out with the Principle Canonical Correlation (PCC) module in PATN.

Results

Site Characteristics

Both the fern gully and the open woodland sites were under a canopy of *Eucalyptus obliqua*, but in the fern gully, the vegetation was much more dense, with *Acacia* and introduced *Ficus* as the understorey, a shrub layer including *Rubus* and *Acrotriche*, with *Gahnia*, *Themeda*, *Pteridium* and *Blechnum* as major components of the ground layer, and large amounts of fallen timber. By comparison, the open woodland had more widely spaced eucalypts (with a few introduced *Pinus* trees), an understorey containing *Banksia*, *Acacia*, *Hakea* and *Exocarpos*, shrub layer of *Epacris*, *Acrotriche* and *Spyridium* and grass layer of mainly *Themeda* and *Danthonia*. In addition, both sites were infested with numerous introduced, weedy shrub, herb and grass species.

Rainfall during the period studied was 137 mm in May, 153.4 mm in June and 133.4 mm in July, with 19, 17 and 18 rain days per month respectively. This compares well with the 1985–1996 twelve year averages of 104.8 mm, 153.9 mm and 169.2 mm, although the May reading was somewhat higher than usual. During the study period the longest time without rain was two periods with no measurable rain for 4–5 days, one each in June and July, although on both occasions trace rainfall was recorded during the period.

Species Patterns

Seventy-three basidiomycete and six ascomycete taxa were collected. The basidiomycete taxa represented five families and were dominated by the gilled fungi. In all, sixteen genera of gilled fungi were identified. A list of those taxa found during the course of the study and their total frequency within each of the main dendrogram groups is presented in Table 1. Species richness for both sites was highest at the start of the study and decreased with time. The fern gully had both higher initial species richness and more variation in the number of species seen on successive visits (Fig. 2). The genera with the highest species richness were *Mycena* (11), *Cortinarius* (11), *Russula* (3) and *Tricholoma* (3).

Table 1. Species present at the Waterfall Gully sites with total number of fruit bodies for each of the seven dendrogram groups (A-G) used for the ordination plot

Numbers in brackets after the dendrogram group are the number of quadrats in the group. Dendrogram groups in which individual species were most commonly present (>20% of the weighted total occurrence) are listed.

Taxon	Group (No. of quadrats)	A (15)	B (23)	C (38)	D (7)	E (39)	F (65)	G (20)
Amauroderma rude (Berk.) Torrend	E,G	—	—	—	1	8	1	5
Campanella sp. A	B	—	41	—	—	—	2	—
Clavaria cinera	F,G	—	—	—	—	—	2	2
Clavaria sp. A	D,E,G	—	—	2	1	5	2	2
Clavulina rugosa Bull.	C,F,G	—	—	10	—	2	35	8
Clavulinopsis amoena (Zoll. & Mooritzi) Corner	C	—	—	38	—	—	13	3

Table 1. Continued

Taxon	Group (No. of quadrats)	A (15)	B (23)	C (38)	D (7)	E (39)	F (65)	G (20)
Clitocybe sp. A	C,D	1	1	—	—	—	—	—
Cortinarius (Dermocybe) clelandii A.H. Sm.	F,G	3	2	3	3	37	5	1
Cortinarius (Myxamicium) lavendulensis Cleland	A	6	1	1	—	4	—	1
Cortinarius (Myxamicum) archeri Berk.	E	—	—	1	—	5	—	—
Cortinarius (Phlegmacium) castaneofulvus Cleland	G	1	3	3	—	3	—	10
Cortinarius (Phlegmacium) microarcheri Cleland	B,F	—	1	—	—	—	10	—
Cortinarius (Telemonia) fibrillosus Cleland	A,D	7	4	4	6	10	3	1
Cortinarius sp. A	C	—	1	5	—	2	—	1
Cortinarius sp. B	G	—	1	3	—	—	—	13
Cortinarius sp. C	A–C	1	4	3	—	—	1	—
Cortinarius sp. D	D	—	—	7	5	—	8	1
Cortinarius sp. E	F,G	—	—	—	—	—	8	3
Crepidotus variabilis (Pers.: Fr.) P. Kumm.	C,F	—	—	4	—	—	7	—
Crepidotus sp. A	A	6	—	—	—	—	—	—
Crepidotus sp. B	B,E,F	—	36	—	—	47	55	—
Discinella terrestris (Berk. & Broome) Dennis	E,G	—	4	21	8	79	72	50
Entoloma lampropum (Fr.: Fr.) Hesler	C	—	—	1	—	—	—	—
Entoloma prostratum (Cleland) E. Horak	C,D	—	—	4	1	—	1	—
Galerina sp. A	B,E	—	2	—	—	1	—	—
Galerina sp. B	F	—	—	—	—	—	2	—
Hebeloma mesophaeum (Pers.) Quél.	F	—	—	—	—	—	2	—
Hydnum repandum L.: Fr	B,F	—	2	—	—	—	15	—
Inocybe sp. A	A,B	13	64	6	—	—	2	—
Inocybe sp. B	B,D,F	—	10	—	4	5	18	—
Laccaria laccata (Scop.: Fr.) Cooke	B,D	2	37	13	23	18	13	1
Lactarius eucalypti O.K. Mill. & R.N. Hilton	F	—	—	—	—	—	1	—
Leotia lubrica Pers.	E	—	—	—	—	7	—	—
Leptonia albida Cleland	A,F	5	2	1	—	3	—	3
Mycena australiana Cleland	B,C,E	—	108	230	—	136	140	3
Mycena cunninghamiana Cleland	E,F,G	—	—	—	—	2	2	1
Mycena fusca Cleland	A	13	10	14	1	16	10	2
Mycena pullata (Berk. et Cooke) Sacc.	C	3	5	42	—	14	4	1
Mycena subgalericulata Cleland	C,D,E	2	53	115	19	139	13	2
Mycena sp. A	D,G	—	1	—	8	4	27	58

Table 1. Continued

Taxon	Group (No. of quadrats	A (15)	B (23)	C (38)	D (7)	E (39)	F (65)	G (20)
Mycena sp. B	G	—	1	7	—	17	22	58
Mycena sp. C	B,E,G	—	1	—	—	2	—	1
Mycena sp. D	F	—	—	—	—	—	1	—
Mycena sp. E	B	—	2	—	—	—	1	—
Mycena sp. F	D	1	106	32	316	75	154	10
Oudemasiella radicata (Relhan: Fr.) Singer	B	—	2	—	—	—	—	—
Omphalina chromacea (Cleland) T.W. May & A.E. Wood	B	1	24	—	—	16	4	—
Panaeolus paludosus Cleland	B	—	2	—	—	—	—	—
Panus lecomptei (Fr.: Fr.) Corner	F	—	—	—	—	—	17	—
Paxillus infundibuliformis Cleland	A	1	—	—	—	—	—	—
Pluteus lutescens (Fr.) Bres.	E	—	—	—	—	205	—	—
Pluteus sp. A	A,C	1	—	1	—	—	—	—
Podoserpula pusio (Berk.) D.A. Reid	F	—	—	—	—	—	1	—
Ramaria ochraceosalmonicolor (Cleland) Corner	C,E,F	—	—	3	—	2	8	—
Rhodocybe reticulata (Cleland) E. Horak	B,E	—	1	—	—	1	1	—
Rickenella fibula (Bull.: Fr.) Raithelh.	D	—	—	—	3	—	1	1
Russula mariae Peck	A,C	1	—	1	—	—	—	—
Russula pectinata Peck	D	—	—	1	1	—	—	—
Russula persanguinea Cleland	B,C,E	—	1	2	—	5	—	—
Stereum sp. A	D	—	—	—	16	2	6	—
Thelephoraceae sp. A	F	—	—	—	—	—	9	—
Tremella mesenterica Retz.: Fr.	E,G	—	—	—	—	8	—	11
Tricholoma sp. A	B,E	—	2	—	—	1	—	—
Tricholoma sp. B	D	—	—	—	1	—	—	—
Tricholoma sp. C	E	—	—	—	—	1	—	—
Tricholomopsis rutilans (Schaeff.: Fr.) Singer	B,D	—	2	3	2	—	—	—
Xylobolus illudens (Berk.) Boidin	G	—	—	—	—	2	—	5
Ascomycota sp. A	C	—	—	6	—	—	—	—
Ascomycota sp. B	E,G	—	—	—	—	6	—	2
Ascomycota sp. C	B,E	—	85	11	—	68	16	9
Ascomycota sp. D	C	—	—	25	—	—	—	—
Basidiomycota sp. A	E	—	—	—	—	4	—	—
Basidiomycota sp. B	E	—	—	—	—	1	—	—
Basidiomycota sp. C	C	—	—	1	—	—	—	—
Basidiomycota sp. D	C	—	—	1	—	—	—	—
Basidiomycota sp. E	G	—	—	—	—	—	—	9
Basidiomycota sp. F	F,G	—	—	—	—	—	1	1
Basidiomycota sp. G	C,F	—	—	4	—	1	12	—

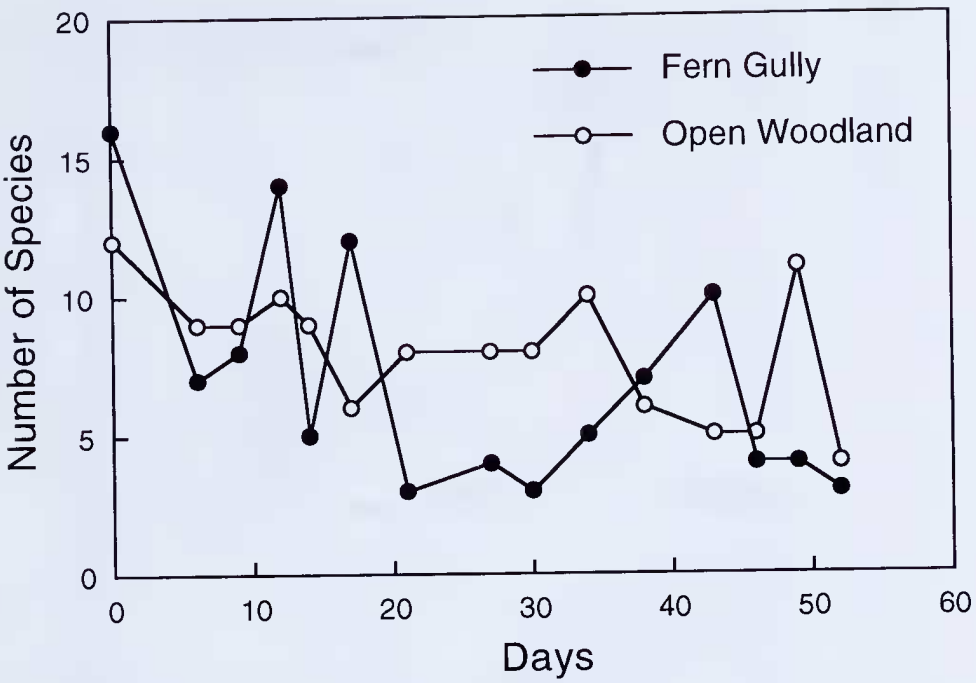

Fig. 2. Total species richness for the Fern Gully and open Woodland sites throughout the study period.

There were four major trends in the frequency of fruiting of those taxa which had a high occurrence of fruit production.

(1) Related species which occurred on similar substrates demonstrated an inverse pattern of high frequencies. For example, *Mycena australiana* and *M. subgalericulata* which grew on large woody substrata exhibited an inverse pattern of abundance: when the number of fruiting bodies of one was low the other was high (Fig. 3a). A similar relationship was observed between two species on *Inocybe* (Fig. 3b), a genus with mycorrhizal taxa (Aberdeen 1979).

(2) Taxa which had a high frequency of fruiting over a short period of time. This was observed in *Pluteus lutescens* which has a short lived peak in number of fruiting bodies. This peak fell off rapidly and the species did not occur again during the sampling period (Fig. 3c).

(3) Some genera were present in low or variable frequencies but were observed both throughout the sampling period and at both sites. For example, Laccaria laccata and several *Cortinarius* and *Mycena* spp. were observed throughout quadrats at both sites for the duration of sampling (Fig. 4a), although *Laccaria* does peak noticeably in the open shrubland.

For all three of these trends there was a general decline in the overall frequency of fruiting over the sampling period, with peaks in abundance being in the first 30 days of sampling.

(4) There was one ascomycete, *Discinella terrestris*, which increased in fruit frequency throughout the sampling period. This trend was observed at both of the sites, although this taxon appeared later within the quadrats in the wetter fern gully site than at the open shrubland site (Fig. 4b).

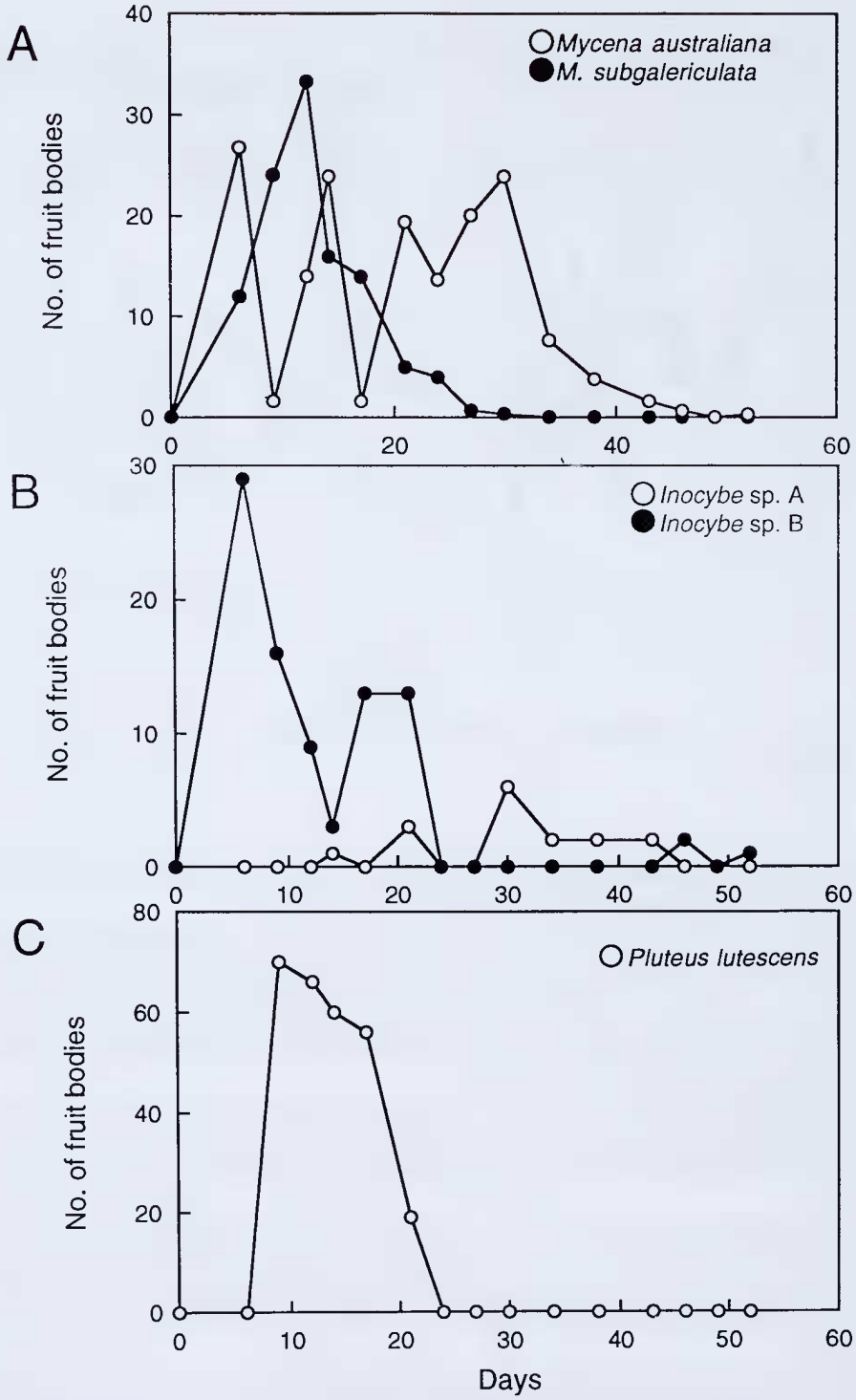

Fig. 3. a–c Examples of some of the phenology patterns exhibited by widespread species. Data represent totals for each species across all sites for each sample: **a** two common species of *Mycena* which grew on large woody substrata and exhibited an inverse pattern of abundance; **b** two species on *Inocybe* which also exhibited an inverse pattern of abundance; **c** *Pluteus lutescens* which showed a high frequency of fruiting over a short period of time.

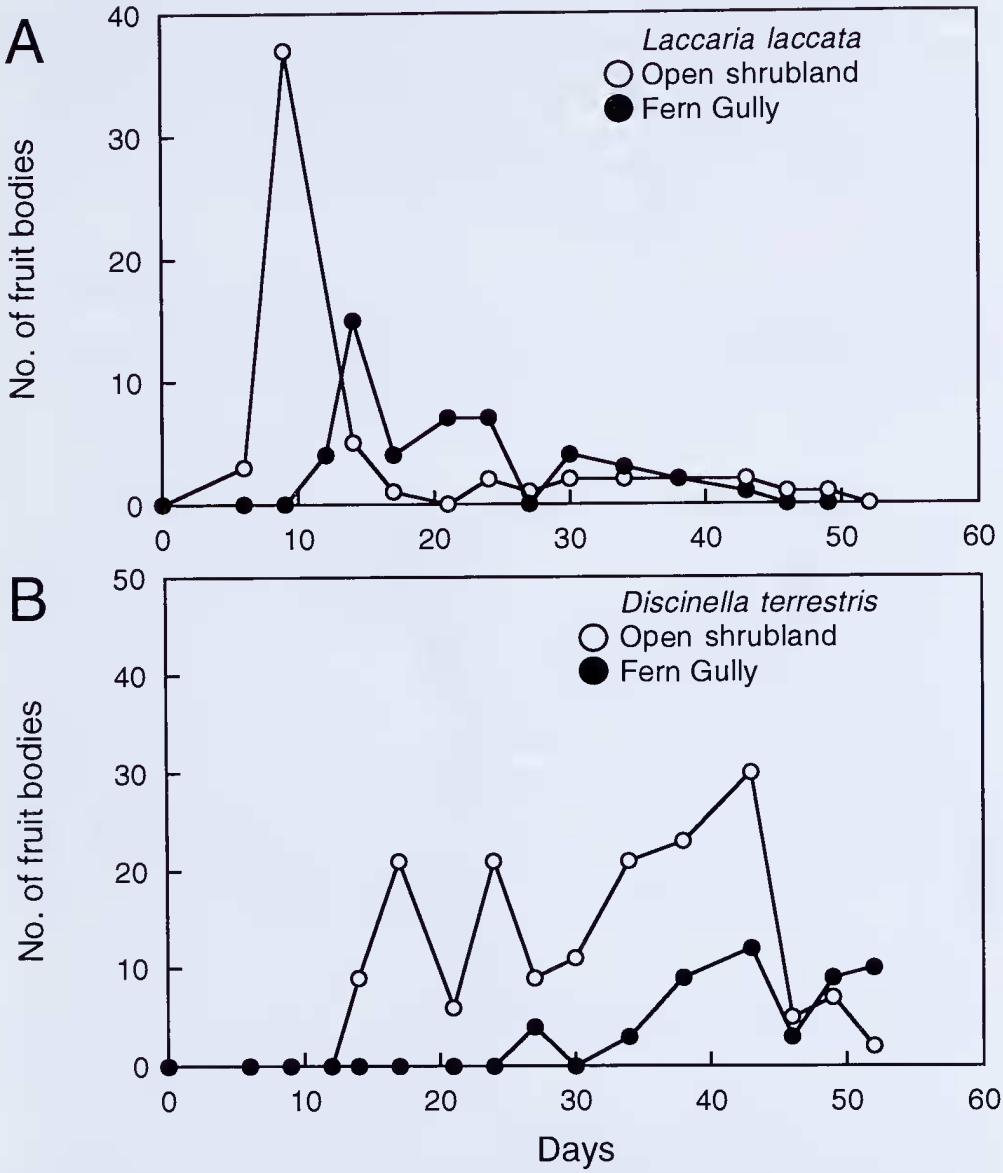

Fig. 4. a–b Examples of the patterns of phenology seen between the fern gully and the drier more open forest sites: **a** *Laccaria laccata* was observed at low frequencies throughout quadrats at both sites for the duration of sampling; **b** *Discanella terrestris*, increased in fruit frequency throughout the sampling period at both of the sites. This taxon appeared later within the quadrats in the wetter fern gully site than at the open shrubland site.

Cluster Analysis

The dendrogram was truncated at the seven group level. The relationships of these groups to each other are summarised in the inset in Fig. 5. The dendrogram can also be divided into three supergroups, the first (Groups A–D) representing quadrats predominantly from the first nine sample times: Group A represented quadrats 1 and 2 from the

fern gully; Group B was quadrats 3, 4 and 5 of the fern gully; Group C was quadrat 6 from the fern gully and quadrats 1, 2 and 4 from the more open woodland; and Group D represents quadrat 5 from the open woodland. The second supergroup (Group E) consists of a mixture of quadrats 1 and 2 from the fern gully (times 10–15) and open woodland quadrats 6–8, times 1–9. The third supergroup (Groups E–F) represents quadrats from times 10–15. Group F is made up of fern gully quadrats 3–8 and open woodland quadrats 1–5; Group G, open woodland quadrats 6–8 only.

The species found in the survey which were found to be either restricted to or most common in particular dendrogram groups, were as follows:
Group A: *Cortinarius lavandulensis*, *Crepidotus* sp. A and *Paxillus infundibuliformis*.
Group B: *Campanella* sp. A, *Oudemansiella radicata*, *Omphalina chromacea* and *Panaeolus paludosus*.
Group C: *Clavinulopsis amoena*, *Cortinarius sp.* A, *Entoloma lampromum*, *Mycena pullata*, Ascomoycota spp. A & D and Basidiomycota sp. D.

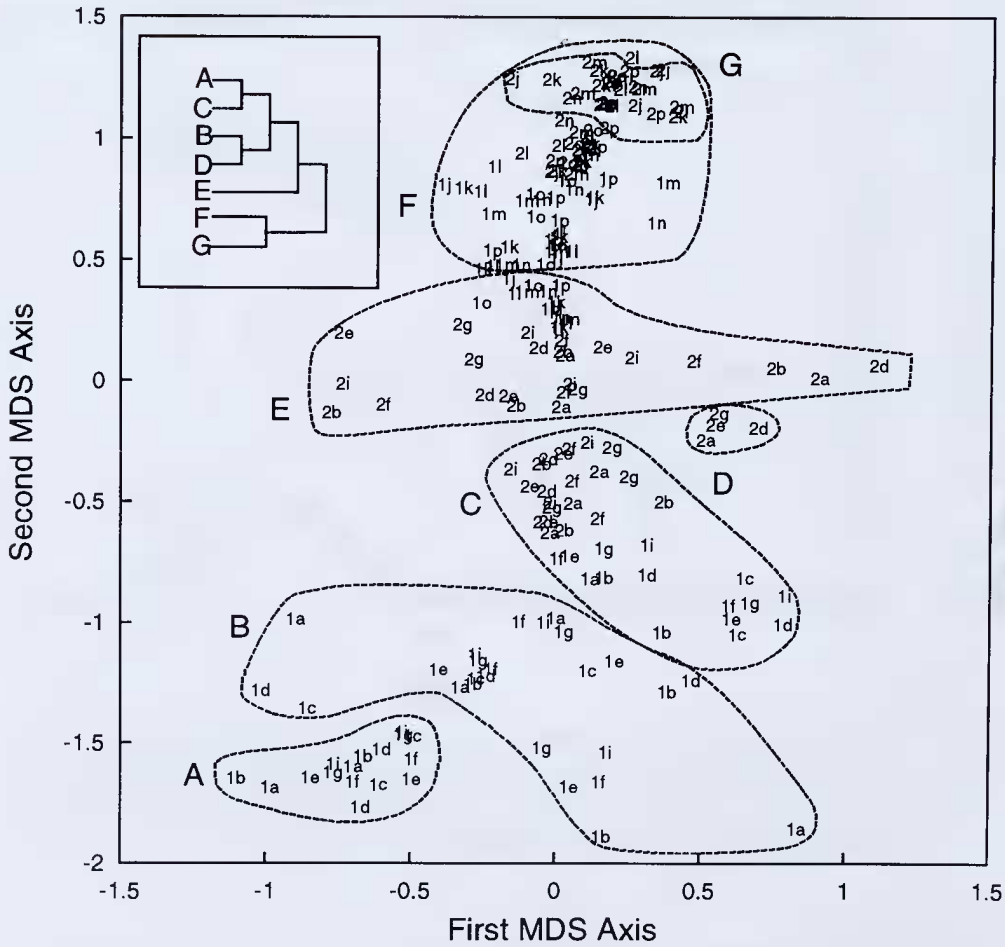

Fig. 5. MDS Ordination of the quadrats sampled through time with seven equally dissimilar dendrogram quadrat groups (A–G) identified from Bray-Curtis, UPGMA clustering (inset). Within the groups, 1 and 2 represent quadrats from fern gully and open forest sites respectively, lower case a-p represent the repeated observations through time for each site from earliest to latest.

Group D: *Cortinarius* sp. D, *Mycena* sp. F, *Rickenella fibula*, *Russula pectinata*, *Stereum* sp. A and *Tricholoma* sp. B.
Group E: *Cortinarius archeri*, *Leotia lubrica*, *Pluteus lutescens*, *Tricholoma* sp. C and Basidiomycota spp. B & E.
Group F: *Galerina* sp. B, *Hebeloma mesophaeum*, *Mycena* sp. D, *Panus lecomptei*, *Podoserpula pusio* and Thelophoraceae sp. A.
Group G: *Cortinarius* sp. B, *Mycena* sp. B, *Xylobus illudens* and Basidiomycota sp. E.

Ordination

The MDS ordination restricted to two dimensions produced a stress value of 0.12. This stress value is considered to represent an acceptably small degree of distortion of the inter-OTU (operational taxonomic units) distances. MDS (unlike Principal Component Analysis) does not partition the variance along the principal axes and all axes contribute equally, so alignment or greater spread along the 'second' axis is not a concern (Belbin 1992).

When the dendrogram groups were overlaid on a plot of these two ordination dimensions (Fig. 5), five groups (A–F) were discrete, with two groups (F and G) overlapping. The ordination groups aligned mostly along the second MDS axis, with the lower quadrants representing the early season samples, when conditions were generally wetter and warmer. When the dendrogram groups were compared with the PCC vectors for the environmental features measured (Fig. 6), Groups A and B were associated with recent rainfall events, whereas quadrat Groups C and D were related more with the amount of rain and higher temperatures. Rainfall, and temperature show a similar second MDS axis response, decreasing in intensity, with Group F representing drier and cooler (and later) sites. However, this relationship is inversely related to sampling time which increases across Groups B, C, D to F, and therefore rainfall, temperature, and time of sampling are confounded and cannot be distinguished uniquely as discrete factors underlying community structure. The number of days since last rain increased in the direction of Group A to F and G, indicating that fungi in Group A, and to a lesser extent Group B, tended to be associated with recent rainfall while other Groups did not.

The quadrats in Group E were aligned along the first MDS axis and were not clearly associated with the most of environmental features measured. There was a tendency for the soil moisture and species richness features to align with this axis, but they represent non-significant trends only.

In summary, five patterns of quadrats were seen in relation to environmental variables: (1) those occurring early during sampling, which corresponds to wet warmer conditions (dendrogram Groups A–D), (2) those occurring late during sampling corresponding to drier cooler conditions (Groups F–G), (3) those occurring after recent rainfall (Groups A and B), (4) those occurring without recent rainfall (Group G), and (5) quadrats which were not correlated significantly with any of the environmental variables measured (Group E).

Group D was unique in that it only contained representative temporal samples of a single quadrat from the shrubland site for the first 33 days of sampling. It was observed that this quadrat had a homogeneous species richness and high abundance throughout the first half of the sampling period. Although there were no significant relationships between species richness, abundance or soil moisture within the ordination space, these factors showed a general trend of increasing influence in the direction of group D (Fig. 5).

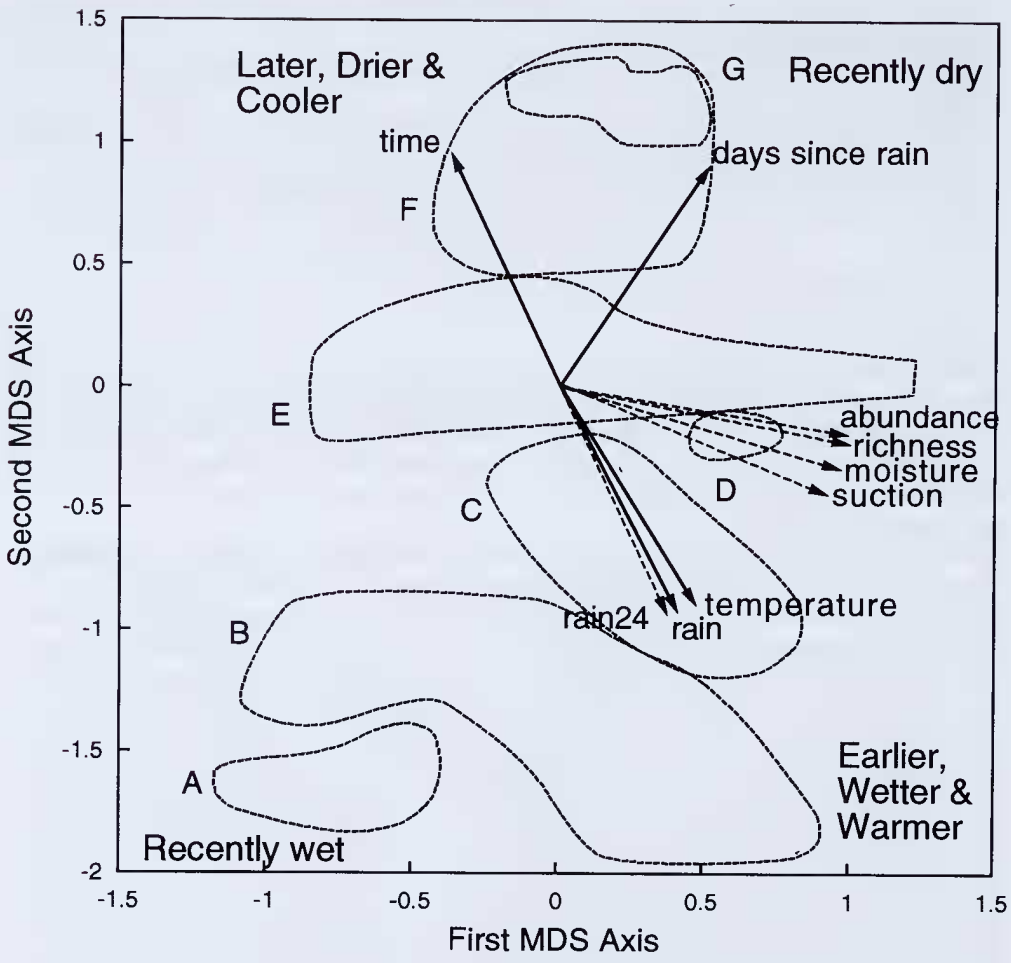

Fig. 6. The relationships between the quadrats and the measured environmental variables are shown as PCC vectors; significant correlations are indicated by solid vector lines, non-significant trends by dashed lines; vector directions indicate the direction of increasing effect within the ordination space. Group positions and letters are those from Fig. 4.

Discussion

A large number of fungal species were found in Waterfall Gully from late autumn to mid winter of 1992. Although most species were present throughout large parts of the sampling period, many species only produced one or two fruiting bodies during this time, with only a few taxa both common in number and through time. This pattern of a few major taxa accounting for most biomass has also been documented for ectomycorrhizal basidiomycetes (Bills *et al.* 1985).

There was a strong temporal influence on the fruiting pattern which correlated with the rainfall and temperature fluctuations during the sampling period. Early in the season there were differences in the fungal composition between the sites, but their composition converged during mid-winter. Due to the relationship between rainfall, temperature and time, these factors could not be distinguished in isolation as having the greatest influence on the structure of the fungal community. The temporal pattern may have resulted from ambient conditions as other studies have related the intensity of fruiting to

ambient temperature and moisture availability (e.g. Austwick 1968; Blackwell and Gilbertson 1984). A full seasonal study would be required to elucidate the latter, and studies often require several years to isolate environmental factors from temporal patterns (Peterson 1977; Mehus 1986).

For example, in the basidiomycete *Dermocybe uliginosa* the onset of fruit body production was found to be initiated by soil temperature at 0.05m and the daily minimum temperature above the soil surface whereas the abundance of fruiting bodies may also be determined by the soil water vapour pressure (Kotilová-Kubicová *et al.* 1990). Initiation of spore production in the ascomycete *Venturia inaequalis* (St-Arnaud *et al.* 1985) and fruit body production of the basidiomycete *Lactarius mexicanus* (Luz and Torres 1994) were also strongly correlated with minimum ambient temperature and specific sustained levels of precipitation. Similarly, individual myxomycete species demonstrated resource partitioning through temporal variation in sporulation along moisture and canopy cover gradients (Stephenson 1988).

It is interesting that as conditions at Waterfall Gully became cooler, albeit slightly drier, there was convergence in the fungal floras across the open and closed forest-type quadrats. Mehus (1986) found that in good fungal seasons in Scandinavia (equivalent to cool and wet winters in South Australian terms) there is more similarity in the fungal species composition between different sites than in dry years. Salo (1994) working in Finnish forests also found that their communities were dominated (as were ours) by *Cortinarius*, *Mycena*, *Tricholoma* and *Russula* spp. and that species diversity was higher in the more mesic environments sampled, especially for mycorrhizal and saprophytic macrofungi. Similarly, G'osheva and Bogoev (1990) in Bulgarian pine forests found that phenology was strongly controlled by humidity and microclimate.

Holownia (1986) observed that within apparently 'uniform' ecological communities, there were different patterns of fungal fruit body emergence, with the same species behaving differently in different, but closely spaced areas sampled, concluding that this was the result of edaphic responses. In that four year study, several species were found to be reliably predictable in their fruiting rhythms, whereas other taxa exhibited two- or three-phase fruiting appearances which were considered to be responses to temperature and moisture rather than species-specific characteristics. In contrast, Fedora and Boobook (1986) found that *Armillariella mellea* was only capable of fruiting once per season on the same substrate, although the environment and climate also influenced the timing of the fruiting.

We found that at Waterfall Gully as conditions became generally drier, there was convergence in the fruit body types emerging at the sites, but as this was associated with a general reduction in total species numbers, it possibly represents convergence through all sites becoming sufficiently dry that only those species which can produce fruit bodies under lower moisture levels were observed. This was further seen in the split into those quadrats sampled before and after time 9 of the study. These later samples were drier and generally more similar floristically. The earlier sampled quadrats were wetter and there was patchiness not only between the fern gully and shrubland sites, but also between different quadrats within these sites. This suggests that there are microclimatic or at least microecological features which are influencing the appearance of the fruit bodies. Nevertheless, as with the studies of Mehus (1986), Stephenson (1988) and Salo (1994) the highest species diversity, richness and total abundance were in the more mesic sites at the wettest times.

The quantitative effects of cover were not measured in this study, and should be the subject of further studies to determine how exposure influences not only fruit body production, but also the other environmental parameters which themselves can affect fungal phenology. Similarly, the potentially differential phenology responses to the

environment by soil-living mycorrhizal versus wood-rotting fungi need more careful investigation. Nevertheless, there were both mycorrhizal (e.g. *Cortinarius* and *Russula*) and wood-rotting taxa (*Mycena* and *Pluteus*) present as key species in several of the dendrogram groups, suggesting that the responses were not necessarily substrate specific.

Soil moisture was not a good indicator of water availability to the fungi, as many species grew on other substrata. Methods of quantifying the moisture content of substrata other than soil, such as leaf litter and logs would allow for a better evaluation of the importance of moisture in fungal fruiting. The moisture holding capacity of substrata can influence the persistence time of the fruiting structure (Ingold 1984). The water content of leaf litter and fine twigs is primarily a function of daily temperature and relative humidity. In contrast, branches, logs and stumps take longer to dry after being saturated by heavy rains. Larger substrata also provide greater organic carbon supplies than smaller substrata (Mehus 1986). These larger substrata may form a suitable surface for continuous fruit production and lead to more competitive influences structuring the community. Relationships between different species of *Mycena* and *Inocybe* which grew on logs and stumps may have resulted from this.

There are also many fungal species which may have mycorrhizal associations, and in a number of studies it has been observed that the interaction between the host and the symbiont is also important in fungal phenology (Bentivenga and Hetrick 1992; Johnson-Green *et al.* 1995), thus the mycorrhizal status of the fungal taxa observed in the present study requires clarification. The fungal response to the mycorrhizal partner, site location and substrate age and condition were all considered to interact in determining the ecology of the taxa observed by Holec (1993), and careful experimental design will be needed as well as longer-term observations to unconfound the effects of the parameters affecting fruiting phenology at Cleland.

In the Waterfall Gully area, there are indications of relationships between environmental factors and the patchy distribution of many macrofungal species. Further investigations are required in particular, long term studies or permanent sites, combined with more detailed measurement of ecological parameters and potential mycorrhizal interactions before the observed patterns can be explained adequately.

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